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Behavioral correlations across activity, mating, exploration, aggression, and antipredator contexts in the European house cricket, *Acheta domesticus*

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Abstract Recently, there has been increasing interest in behavioral syndrome research across a range of taxa. Behavioral syndromes are suites of correlated behaviors that are expressed either within a given behavioral context (e.g., mating) or between different contexts (e.g., foraging and mating). Syndrome research holds profound implications for animal behavior as it promotes a holistic view in which seemingly autonomous behaviors may not evolve independently, but as a “suite” or “package.” We tested whether laboratory-reared male and female European house crickets, *Acheta domesticus*, exhibited behavioral syndromes by quantifying individual differences in activity, exploration, mate attraction, aggressiveness, and antipredator behavior. To our knowledge, our study is the first to consider such a breadth of behavioral traits in one organism using the syndrome framework. We found positive correlations across mating, exploratory, and antipredatory contexts, but not aggression and general activity. These behavioral differences were not correlated with body size or condition, although age explained some of the variation in motivation to mate. We suggest that these across-context correlations represent a boldness syndrome as individual risk-taking and exploration was central to across-context mating and antipredation correlations in both sexes.

Keywords Personality · Boldness · Temperament · Behavioral syndromes · Risk-taking

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Over the past 5 years, behavioral ecologists and evolutionary biologists have witnessed a dramatic upsurge in behavioral syndrome research (Sih et al. 2004b; Bell 2007; Sih and Bell 2007). Succinctly defined, behavioral syndromes are suites of correlated behaviors expressed either within a given behavioral context (e.g., foraging) or between different contexts (e.g., foraging and antipredator behavior; Sih et al. 2004a, b). Behavioral syndromes hold profound implications for studies of animal behavior as they advocate a holistic view of behavior in which seemingly autonomous behaviors may not evolve independently, but as a “suite” or “package” (Price and Langen 1992; Sih et al. 2004b). As such, selection affecting one behavior in the suite may also affect how other behaviors are expressed across behavioral contexts (Sih et al. 2004b; Sih and Bell 2007). The ramification is that behaviors may not be free to evolve adaptively to independent optima across contexts due to underlying physiological, behavioral, or genetic constraints associated with the syndrome. Thus, the framework of behavioral syndromes has the potential to revolutionize the manner by which we study animal behavior, particularly if syndromes are common across taxa. The ecological and evolutionary importance of behavioral syndromes is increasingly being recognized both empirically (e.g., Bell 2005; Dingemanse et al. 2007; Wilson and McLaughlin 2007) and conceptually (Sih et al. 2004b) as noted in a recent review by Bell (2007).

Personality traits (e.g., boldness, sociability, aggressiveness, activity) are difficult to study in isolation as they often incorporate multiple types of behavior in different contexts and/or situations (Bell 2007; Réale et al. 2007). For example, boldness has been defined as an individual’s tendency to take risks (Ward et al. 2004; Réale et al. 2007) and/or be exploratory in novel contexts (Wilson et al. 1994;

Wilson and Stevens 2005). Boldness has been observed in a number of ecologically relevant behavioral paradigms, including those associated with risk-taking and antipredator behavior (e.g., Godin and Davis 1995; Kortet and Hedrick 2007; Wilson and Godin 2009), mate choice (e.g., Godin and Dugatkin 1996), activity (e.g., Wilson and McLaughlin 2007), aggression (e.g., Huntingford 1976), dispersal (e.g., Fraser et al. 2001; Rehage and Sih 2004), and learning (e.g., Dugatkin and Alfieri 2003), as well as foraging and exploration (e.g., Wilson and Stevens 2005). Furthermore, a handful of studies have provided evidence that boldness can be correlated with fitness-related factors (Smith and Blumstein 2008), heritable (Drent et al. 2003), and subject to natural selection (Réale and Festa-Bianchet 2003; Dingemanse and Réale 2005 and references therein).

While little doubt remains that personality traits such as boldness exist across animal taxa, the contextual nature of these behaviors and their adaptiveness continues to be a subject of contention. Some studies advocate an adaptationist perspective in which boldness is free to evolve and be expressed optimally within each context (Webster et al. 2007). In contrast, other studies advocate a syndrome perspective, which favors evolutionary constraint to adaptation. This perspective posits that a behavior may not be free to evolve optimally due to underlying constraints (Johnson and Sih 2005). The conundrum has primarily to do with the contextual nature of boldness. Is boldness consistently expressed across contexts, or does it vary? Similarly, if boldness is best characterized in a syndrome, what types of behaviors are correlated with it and what types are not? Evidence for boldness being both context-specific (Coleman and Wilson 1998; Wilson and Stevens 2005; Webster et al. 2007) and context-general (Dochtermann and Jenkins 2007) is readily available. Thus, there is much to be gained from a comparative method of assaying which behaviors are correlated with one another, or not at all, across taxa. Understanding the contextual nature and taxonomic expression of boldness and other personality traits, therefore, remains an important area of research need.

The syndrome literature has grown extensively in recent years (Sih et al. 2004b), particularly in mammals (e.g., Martin and Réale 2008), birds (e.g., Quinn and Cresswell 2005), reptiles (e.g., Stapley and Keogh 2005), and fish (e.g., Moretz et al. 2007; Wilson and McLaughlin 2007; Wilson and Godin 2009). These last few years have also seen growth in syndrome research on invertebrates, though to a somewhat lesser extent than vertebrates. For example, there have been several studies on arachnids (Riechert and Hedrick 1993; Johnson and Sih 2005; Johnson and Sih 2007), cephalopods (Sinn et al. 2008), and insects (Hedrick 2000; Sih and Watters 2005; Kortet and Hedrick 2007). Two of these recent studies have focused on crickets. Hedrick (2000) revealed that male western stutter-trilling

crickets, *Gryllus integer*, that produce conspicuous mate attraction displays compensate with increased antipredatory behavior. Conspicuous callers take longer to emerge from a shelter when placed in a novel environment and also stop calling for longer periods of time when their calling is interrupted by cues from a potential predator (Hedrick 2000). Furthermore, Kortet and Hedrick (2007) showed that male *G. integer* exhibit an aggressiveness/activity syndrome. Intrasexual aggression (male–male) was correlated with activity level in a novel environment. Together, these studies suggest that *G. integer* exhibits a boldness syndrome. These studies prompt further investigation into the importance of boldness in male and female crickets.

In this study, we ascertain whether commercially bred European house crickets, *Acheta domesticus*, exhibit a boldness syndrome. Wild male crickets compete in aggressive interactions (contests) to gain access to a mate attraction territory (Alexander 1961). They then stridulate, producing a series of long-distance chirps (calling song) that functions to attract females from a distance (phonotaxis). Upon attracting a female, males produce courtship song. Female crickets generally select their mate based on body size, fighting, and singing ability (Crankshaw 1979; Gray 1997; Nelson and Nolen 1997). Captive-bred crickets display similar male aggressiveness, calling, courtship, and female mate choice behaviors as their wild counterparts. They differ from wild crickets in that wild crickets are also exposed to an assortment of natural predators (i.e., numerous insectivorous invertebrates and mammals; Hedrick and Kortet 2006; Bertram, personal communication). Crickets exposed to predators exhibit a variety of antipredatory behaviors including retreating into a sheltered area (crack in the ground or vegetative cover) when they sense the approach of a predator (Hedrick and Kortet 2006; Bertram, personal communication) and self-amputating (autotomizing) an entrapped leg to escape a predatory attack (Bateman and Fleming 2005, 2006a, b; Fleming and Bateman 2007). It is presently unknown whether captive-bred crickets exhibit these antipredatory strategies.

We investigated correlations between activity, exploration, antipredatory behavior, aggression, mate attraction displays, and mate phonotaxis. We chose to quantify these six behavioral contexts because they represent a breadth of ecologically relevant behaviors by which to compare against wild populations.

Methods

Experimental holding conditions

A. domesticus crickets were obtained as juveniles from a commercial laboratory supplier (Port Credit Pet Centre,

Mississauga, ON, Canada) and held in six communal 68-L rectangular (64×40×42 cm) plastic containers in an insect-rearing facility in the Nesbitt Biology Building at Carleton University, Ottawa, ON, Canada. Crickets were provided with ad libitum water and food (Harlan Teklad Rodent Diet 8604, Madison, WI, USA) and ample shelter in the form of staggered egg cartons. All crickets were raised under a reversed 12:12 (dark/light) diurnal cycle to facilitate later behavioral observations at a temperature of $21\pm2^{\circ}\text{C}$. All experimental trials were conducted in a dark room under red light to ensure the crickets behaved as naturally as possible and to reduce the risk that the crickets would be startled by the presence of the human observer(s).

Communal containers were checked daily for any individuals that had undergone final molt and, thus, reached adulthood. These adults were immediately transferred to individual 500-ml housing containers (paper ice cream cup with a clear plastic lid). Each housing container included a small refuge, and crickets were offered ad libitum access to food and water. The refuge consisted of a 30-ml plastic cup glued on its side to a 5×6.5-cm metal plate. Two small L-shaped brackets were glued to the front and lateral to each side of the plastic cup to act as a brace for a removable door. The door was a 5×6.5-cm metal plate. The entire refuge was painted opaquely in matte black to ensure consistency between individual containers. Because subjects were kept individually during the experimental period, it is possible that factors associated with motivational state (e.g., lack of mating experience) may have influenced some of the behaviors quantified over the course of the study. We have accounted for this possibility wherever possible in our analyses (see below). That said, solitary housing was an important aspect of our experimental design for two reasons. Firstly, any interaction between experimental subjects (e.g., agonistic/mating interactions) may have had a significant influence on the behaviors being observed that could not be controlled for. Secondly, our experimental design allowed for all individuals to be treated consistently across all behavioral trials therein allowing behaviors across contexts to be compared.

During experimentation, each cricket was put through a series of behavioral trials examining how mate attraction, general activity, exploration, aggressiveness, and antipredator behavior were correlated within and across contexts. We ran 85 females and 71 males through each experiment, except where specified below. At the conclusion of the experimental trials, all individuals were euthanized in a -20°C freezer. Crickets were then dried for 72 h in a drying oven at 60°C and then weighed using a Denver Instruments P1-114 balance.

Behavioral measures

Mate attraction context: calling behavior

On day 1 of the behavioral trials, each male cricket ($N=71$ males aged 12 ± 3 days post final molt) was placed into an electronic acoustic recorder (EAR) system to record individual differences in calling effort. Crickets were kept in their individual containers and so had continual access to their refuge, food, and water. Individual container lids were exchanged with new lids that enabled us to insert microphones inside each container to monitor long-distance mate attraction calls (calling song).

The EAR system consisted of 256 individual compartments. Each individual compartment possessed a small microphone situated approximately 5 cm above the base of the individual's container. Each microphone took eight readings per second wherein a value of 1 was recorded when the cricket was calling and a value of 0 if the cricket was not calling. Each second, the eight readings were summed together, producing a score from 0 to 8. In this way, the EAR system amplified, filtered, and recorded each individual's calling behavior over a period of four nights. Each of the 256 individual compartments was separated by 7 cm of acoustic foam to ensure there was no sound leakage across microphones. Although each microphone only recorded the male in the individual container, not nearby calling males, males could likely hear the calling songs of conspecifics. While this approach may be problematic if the calling of neighbors stimulates some males to call while inhibiting calling in others, it allows for a natural measure of calling effort as male spacing in the wild suggests that they can hear each other. For a more in-depth description of the EAR system, see Bertram et al. (2004). All males were removed from the EAR experimental set-up prior to introduction to measure 3 on day 5.

Male calling effort was quantified in three different ways: average total nightly calling time (time spent calling over each 24-h period, averaged across the 4 days); average bout length (average amount of time calling continuously without taking at least a 1-min break); and average calling bout rate (average number of calling bouts the male produced over the course of each 24 h). These data were collected using a MatLab algorithm that analyzed the second by second raw data collected from the EAR system (available in Bertram et al. 2004).

Mating and exploratory context: phonotaxis

On day 4, individual virgin female crickets ($N=85$ females aged 15 ± 3 days post final molt) were placed inside their

refuge with the door closed. Individuals were then moved to a novel environmental arena to quantify differences in latency to exit the refuge and approach speakers (novel objects) playing conspecific calls. The experimental arena consisted of a black, 17-cm deep plastic trough (76×14 cm at base, 82×18 cm at top) with two black speakers (10×7.8×18.5 cm) at either end of the trough. One speaker (randomly chosen for each female) emitted a two-pulse call, while the other emitted a four-pulse call. The same two-pulse and four-pulse calls were played to each female. Prior to the onset of each experimental trial, the female's refuge (female within, closed door) was placed equidistant between the two speakers. Speakers were calibrated so that the amplitude of each call was 57 dB at the female's refuge. The direction of the refuge's opening was perpendicular to both speakers. The base of the arena was uniformly covered in approximately 2 cm of beige sand.

After allowing the female to acclimate for 3 min inside its refuge with the calls broadcasting, the refuge door was carefully removed and individual differences in latency to exit the refuge were quantified. A female's exit was defined as the time required for her entire abdomen to exit the threshold. Upon exiting, we quantified each female's latency to approach and touch one of the speakers (representing an additional measure of exploration and mate choice/novelty) with their antennae. Note that the time to touch one of the speakers was completely independent of the emergence time. For example, an individual that took 50 s to emerge from the refuge and 10 s to touch the novel object was scored as 50 and 10, not 50 and 60 s. Trials were terminated after 3 min for females that did not emerge from the refuge or a further 3 min post emergence if the female did not touch the speaker. At the conclusion of each trial, females were returned to their individual housing container together with their refuge. Between trials, sand within the experimental arena was thoroughly raked to reduce the influence of any olfactory cues on subsequent individuals' behavior.

Two-pulse and four-pulse synthetic calls were broadcasted as they represent the natural range of variation in *A. domesticus* (Stout et al. 1983; Stout and McGhee 1988). We purposely did not include a three-pulse call because previous research revealed apparent stabilizing selection via female preference for pulse number; females prefer three-pulse calls to calls with either two or four pulses (Stout et al. 1983; Stout and McGhee 1988; Gray 1997). Because our goal was to assess female exploratory behavior and phonotaxis, not mate preferences, we used background calls that the females would recognize, but would not be overly attracted to. Similar to the findings of Stout et al. (1983), females in our experiment did not

prefer one call type to the other (36 selected the two-pulse call, 39 selected four-pulse call, and 10 did not make a selection).

Exploratory context: exploratory behavior in absence of auditory cues

On day 5, all individuals ($N=71$ males and $N=85$ females aged 16 ± 3 days post final molt) together with their refuge were placed singly into a novel environment arena to quantify individual differences in latency to exit their refuge and explore a novel object. The experimental arena consisted of a 36×19×11.5-cm gray Sterilite plastic container. Note that none of the individuals had any previous experience in this novel environment; it was a completely different design from that used in female phonotaxis to ensure its novelty. A closed-end PVC pipe (3.2 cm diameter×5 cm) was located centrally on the far right end of the Sterilite container. This PVC pipe acted as both a novel object and potential alternate refuge. The base of the arena was uniformly covered in 2 cm of beige sand. Prior to the onset of the trial, an individual's refuge (cricket within, closed door) was placed on the opposite side of the arena with the refuge opening facing the novel object. After allowing the cricket to acclimate for 3 min, the door was carefully removed and individual differences in latency to exit the refuge, explore an open (risky) area, and then touch a novel object/alternate refuge were quantified. Novel object exploration is a fairly common behavioral measure in studies of animal personality and has been suggested to be associated with dispersal, the exploration of novel environments, general activity, and antipredator behavior (see Réale et al. 2007 and references therein). Arena maintenance, trial duration and termination, and quantification of latency to exit and explore the novel object were the same as that described in the mating and exploration context above. Upon completion of this exploration context assay, individuals immediately experienced a predatory event (see below).

Antipredatory context: latency to emerge following a simulated predation event

At the conclusion of the previous assay, any individuals that had exited their refuge volitionally were manually recaptured and returned to their refuge with the door closed. While manual capture would in itself likely act as a simulated predation event, we also used a 30-cm wooden rod to tap on the refuge for 10 s to enhance the predation threat. The cricket was then given 20 s to reacclimate prior to the door being removed. We then quantified latency to exit as described above. At the

conclusion of each trial, crickets were returned to their individual containers.

Activity context: general activity in a novel arena

On day 6, all crickets ($N=69$ males and $N=80$ females aged 17 ± 3 days post final molt) were placed individually into a novel circular arena to measure general activity (walking forward, turning, walking backward, and climbing). The arena consisted of a 1-m closed loop of clear vinyl tubing (2.54 cm outside diameter; 1.91 cm inside diameter) with the ends attached via the use of a 5-cm long piece of vinyl tubing (3.18 cm outside diameter; 2.54 cm inside diameter). Prior to the onset of testing, arenas were placed on a sand substrate and crickets were given 5 min to acclimate to their surroundings before the onset of testing. This acclimation period also prevented the possibility that an escape response would inadvertently be quantified as general activity. Individual differences in general activity (time spent walking, turning around, climbing, and moving in reverse) were then quantified.

Aggression context: aggressiveness towards conspecifics

On day 7, individual male crickets ($N=70$ males aged 18 ± 3 days post final molt) were weighed on a precision analytical balance (model P-114) and then paired with approximately size-matched individuals (35 pairs in total). Paired individuals were placed in a novel arena to quantify individual differences in aggression towards conspecifics. Each male was identified by a small dot of paint (Testors enamel model paint) on its pronotum to allow individual identification during the trial. Trials were held in the same arenas as those described in the exploration assay; however, the novel object/shelter was removed. A paper divider was placed in the middle of the arena, and the two male crickets were placed on either side of the divider. Trials began when the divider was removed. Each trial ran for 3 min and the amount of time each male spent producing aggressive chirps, flaring his mandibles, biting, and grappling with his opponent was quantified. The aggressive measures we quantified are similar to those developed by Alexander (1961) and subsequently modified by Hofmann and Schildberger (2001).

It is important to note that both participants in each fight were subjects in the current study. Because the two males within the trial are not acting independently of each other, there are possible pseudoreplication effects. To reduce these effects, we ensured that the average weight difference between the two opponents was $<10\%$ of the cricket's body weight (average weight difference = 30.59 mg, average body size = 335.42 mg). On the rare occasions where the weight

difference exceeded 20%, those pairs were excluded from aggression analyses ($N=3$ pairs).

Antipredatory context: latency to limb autotomization

On day 8, all individuals ($N=71$ males and $N=85$ females aged 19 ± 3 days post final molt) were exposed to a simulated predation event wherein latency to volitionally autotomize a hind limb was quantified. Each individual was manually captured and placed head first into a glass test tube (1 cm diameter) containing a ball of cotton gauze approximately 2 cm from the opening. This positioning allowed easy access to hind limbs while restricting the movement of the cricket such that nonvolitional limb loss/damage would be minimized. One hind limb was randomly selected and grasped with forceps. The individual was then placed in the experimental arena described in the aggression assay. While still grasping the limb with forceps, the test tube was removed and individual differences in latency to autotomize a limb were then quantified. Trials terminated once an individual autotomized a leg or the trial reached a maximum of 30 s.

Antipredatory context: individual latency to re-emerge following predation event

Immediately following the last antipredatory measure (day 8), individuals ($N=71$ males and $N=85$ females aged 19 ± 3 days post final molt) were manually recaptured, placed back within their refuge (door closed), and returned with their refuge to the experimental arena. Individuals were then given 20 s to acclimate wherein the door was removed and individual differences in latency to emerge following limb autotomization were quantified. Latency to emerge was quantified as described in the mating and exploration assay.

Size and condition measures

Immediately following the last antipredatory measure (day 8), individuals were manually recaptured, placed in a freezer, and humanely euthanized. Male ($N=63$) and female ($N=77$) body morphology was later measured by using the Zeiss dissection microscope Discover v. 12 and Axio Vision software. Note that some individuals were too damaged from storage to obtain body morphology measures. Maximum pronotum width and maximum pronotum length was measured to the nearest 0.1 mm. We used the first principal component of a principal components analysis (PCA) of pronotum width and length as our overall size measure. This first component explained 90% of the variation in the two size traits (Eigenvalue = 1.80). Condition was quantified using resid-

uals from an allometric regression of body mass on body size.

Statistical analyses

To determine whether an across-context behavioral syndrome existed, we ran a PCA for each context (Table 1) and then utilized each first principal component (PC1) in across-context correlation analyses. Data representing each context were incorporated into the PCA (e.g., aggression's PC1 consisted of mandible flare, biting, grappling, and aggressive chirping; calling effort's PC1 consisted of bout duration and bout rate [note that the time spent calling was not included in this PC1 because it is the product of bout duration and rate]; Table 1). Our PCA analyses follow that used by Huntingford (1976) in a landmark paper on across-context behavioral correlations in the stickleback, *Gasterosteus aculeatus*. Following our PCA analyses, we looked for across-context behavioral correlations using nonparametric Spearman's rank correlation tests (r_s). Our correlation analyses match those called for by Bell (2007) in a review of behavioral syndromes. We used a false discovery rate B–Y adjustment ($\alpha < 0.0141$) to account for the 19 correlations that we performed. We opted for the false discovery rate B–Y adjusted alpha instead of the Bonferroni adjustment because the Bonferroni adjustment ($\alpha < 0.0026$ for the 19 correlations) has been shown repeatedly to be overly conservative (e.g., Benjamini et al. 2001; Nakagawa 2004; Narum 2006). Furthermore, we used regression analysis to assess how age, size, and condition influenced each of the

behavioral traits. We used a false discovery rate B–Y adjustment ($\alpha < 0.0128$) to account for the 27 regressions that we performed.

Our results incorporate the data on all individuals, including the ones that did not emerge from their refuge, did not touch the novel object or speaker, and/or did not exhibit leg autotomy (hereafter referred to as nonperformers). Each individual that did not emerge, touch, and/or display autotomy was scored as taking the maximum time possible (180 s for emergence and touch trials, 30 s for autotomy trials) for subsequent data analysis. We included these nonperforming individuals because we did not want to eliminate the more timid individuals from our behavioral syndrome analysis. To determine whether our findings were dependent on the inclusion of these more timid individuals, we re-ran all of our significant statistics after excluding the nonperforming individuals. Overall, our findings were not dramatically changed, except that a few of the correlations that were significant when the timid individuals were included were not when the timid individuals were excluded. These differences are described in the results. A post hoc power analysis revealed that, when the nonperforming individuals were excluded, we did not have sufficient statistical power to ascertain whether the now nonsignificant behaviors were correlated or not.

Results

Most males produced acoustic long-distance mate attraction signals during the 96-h acoustic monitoring period

Table 1 Respective loadings of within-context behavioral variables used to create a principal components score to assess across-context correlations in activity, aggression, mating, exploratory and antipredator behaviors in the European house crickets, *A. domesticus*

Behavioral context	Behaviors within each context	Loadings for PC1	Percent variation explained
Activity	Walking forwards	0.5100	47.19
	Climbing	0.4504	
	Turning around	0.4645	
	Walking backwards	0.5668	
Antipredator	Latency to emerge following predation threat	0.4558	51.07
	Latency to autotomize limb	0.6036	
	Latency to emerge post autotomy	0.6542	
Exploration/silent	Latency to emerge in novel silent environment	0.6930	90.60
	Latency to touch object in novel silent environment	0.7209	
Mating/exploration	Latency to emerge in novel phonotaxis environment	0.7112	89.96
	Latency to touch speaker in novel phonotaxis environment	0.7030	
Mate attraction	Calling bout rate (bouts/24 h)	0.7071	78.40
	Bout length (min)	0.7071	
Aggression	Grappling	0.5318	47.27
	Mandible flare	0.5949	
	Biting	0.4352	
	Chirping	0.4171	

(57 of 71 or 80% of males tested produced calling song). On average, male *A. domesticus* called between 3 and 4 h per night, spent 7.2 min calling without taking at least a 1-min break, and called for 23.1 bouts per day (Table 2). There was extensive among-male variation in all of these traits (Fig. 1a). Male crickets were also very aggressive towards each other, biting and grappling with each other repeatedly, and often producing an aggressive chirp (Fig. 1f).

Female crickets were usually willing to leave their refuge and approach a speaker broadcasting a long-distance mate attraction call (75 of 85 or 88% of females tested left their refuge). There was, however, extensive variation among females in their response times (Table 2; Fig. 1b). On average, for those females that did exit, individuals took 36 s to leave their refuge and 9 s more to approach and touch one of the two broadcasting speakers. Females did not prefer one call type to the other (two-pulse=36, four-pulse=39 females). Furthermore, they did not travel to one call type faster than the other (analysis of variance [ANOVA]: $F_{1, 72}=0.7786$; $P=0.3805$). Similarly, females did not preferentially approach the right speaker over the left speaker (right speaker=36, left speaker=39 females). They also did not travel to one side faster than the other (ANOVA: $F_{1, 72}=0.5930$; $P=0.4438$).

Both sexes displayed a willingness to explore a novel environment (127 of 156 or 81% of the individuals tested

left their refuge during the 3-min observation period). Males and females exhibited extensive among-individual variation in the speed with which they would leave their shelters (Table 2; Fig. 1c). Individuals that emerged quickly from their shelter were also more likely to touch and explore the novel object quickly. Males and females did not differ in the time to emerge from their shelter when no acoustic stimulus was present. However, females emerged from their shelter significantly faster when a mate attraction call was being played (35 ± 4.3 s) than when there was no acoustic stimulus present (53 ± 5.3 s; ANOVA: $F_{1, 147}=6.3307$; $P=0.0129$).

Both sexes also exhibited extensive interindividual variation in antipredatory behavior (Table 2; Fig. 1d). Most individuals self-amputated their leg when captured (autotomy=135/156 individuals). Most were also willing to emerge from their shelter following predation events (banging on the shelter=137/156; autotomy=132/156 individuals). Males and females did not differ in the time to emerge from their shelter following the predation events of banging on the shelter and autotomy, but females emerged 64% faster on average than males following autotomy. Both sexes also displayed considerable variation in their activity levels (Fig. 1e). Females spent more time walking forwards and climbing than males, but the sexes did not differ in their time spent turning around or walking backwards (Table 2).

Table 2 Descriptive statistics (mean \pm SE) for each behavior quantified for males and females using ANOVA

Context	Behaviors within context	Females	Males	<i>F</i>	<i>P</i> value	<i>N</i>
Activity	Walking forwards	56.85 \pm 7.66	26.19 \pm 4.98	10.51	0.0015	149
	Climbing	2.13 \pm 0.54	0.71 \pm 0.34	4.5406	0.0348	149
	Turning around	0.50 \pm 0.15	0.62 \pm 0.20	0.2415	0.6239	149
	Walking backwards	3.61 \pm 0.59	2.25 \pm 0.59	2.6455	0.106	149
Antipredator	Latency to emerge following threat	56.35 \pm 5.57	69.29 \pm 7.64	1.9458	0.165	156
	Latency to autotomize limb	7.83 \pm 1.11	7.97 \pm 1.25	0.0067	0.935	156
	Latency to emerge post autotomy	43.71 \pm 5.38	71.64 \pm 8.05	8.7778	0.0035	156
Exploration/silent	Latency to emerge	69.19 \pm 6.58	80.53 \pm 8.41	1.1599	0.2832	157
	Latency to touch object	36.93 \pm 6.21	58.20 \pm 9.16	3.8961	0.0502	157
Mating/exploration	Latency to emerge	54.16 \pm 6.49				85
	Latency to touch speaker	30.92 \pm 6.43				85
Mate attraction	Calling bout rate		23.13 \pm 2.19			71
	Total nightly calling time		224.23 \pm 26.06			71
	Bout length (min)		7.16 \pm 0.75			72
Aggression	Grappling		3.31 \pm 1.10			70
	Mandible flare		3.96 \pm 0.64			70
	Biting		5.24 \pm 1.48			70
	Chirping		17.10 \pm 2.50			70

Behaviors that differ significantly ($\alpha<0.05$) between the sexes are identified in italics. For those measures quantifying latency to emerge from a refuge, all individuals (performers/nonperformers) for both males and females are included

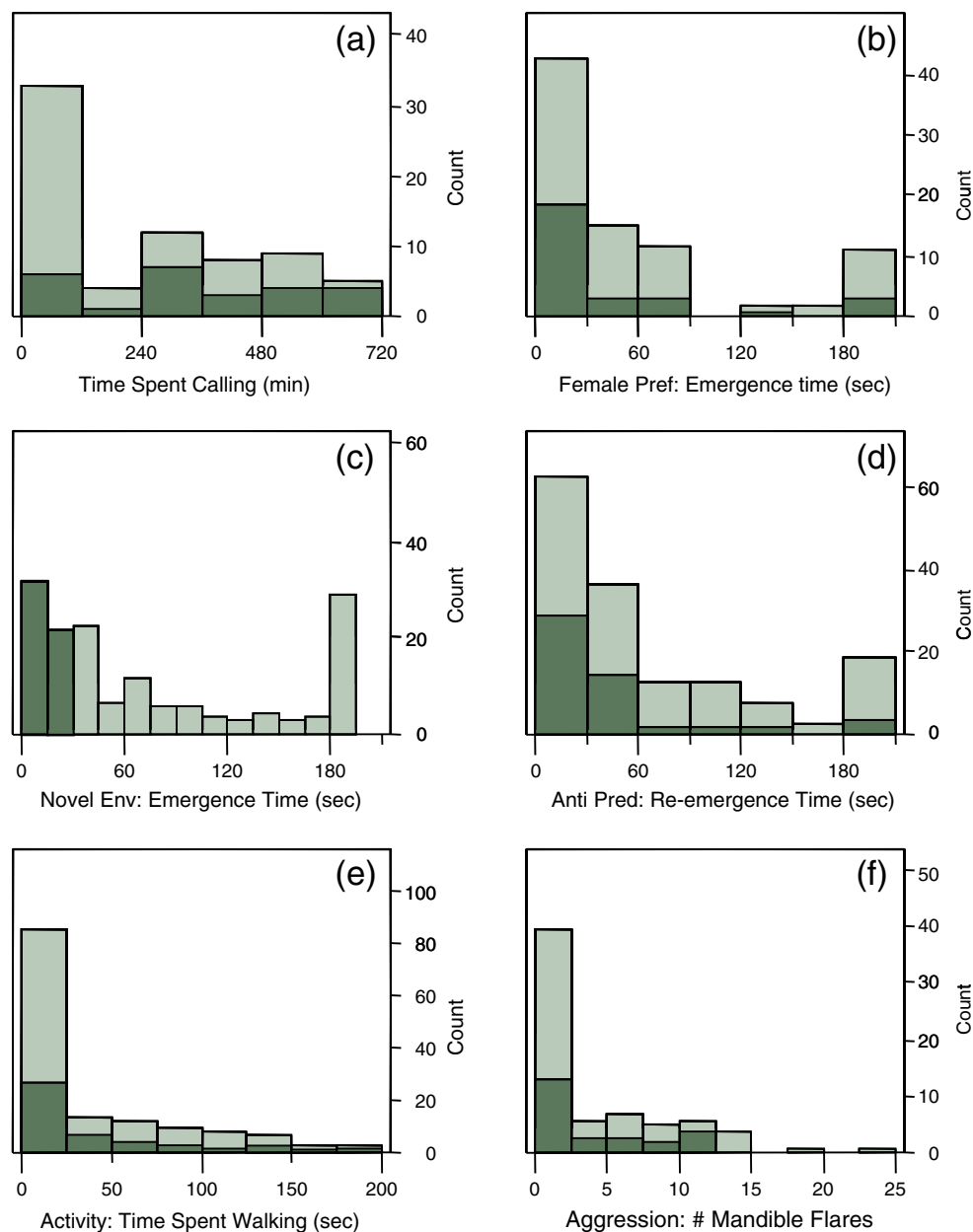


Fig. 1 Plots showing the among-individual variation in six different behavioral contexts; one representative behavior from each context was chosen. **a** Mate attraction: average nightly calling time (in minutes); **b** phonotaxis: female preference emergence time (in seconds); **c** novel environment: emergence time; **d** antipredatory: re-emergence time following first predation event; **e** activity: time spent walking forwards and backwards in arena; and **f** aggression: number of mandible flares observed. The *darker shaded portions* of the graphs in **a–d** represent the most exploratory (boldest)

individuals (i.e., the individuals that emerged from their shelter in a silent novel environment within 30 s of starting the novel environment experiment). The more exploratory (bolder) individuals are not shaded dark in **e** and **f** because exploration behavior was not correlated with either activity or aggression (see Table 2). **a–d** show that the more exploratory (bolder) individuals spend more time signaling through the course of the night, emerge quicker in phonotaxis trials, and emerge quicker in antipredatory trials than the less exploratory individuals

Across-context behavioral correlations

Mating and exploratory behaviors were significantly correlated in both sexes (Table 3; Fig. 2a, b). Males that were more exploratory (quickly exited their refuge and touched the novel object) exhibited greater overall calling effort

(called for longer periods of time without taking a break and for more bouts; Table 3; Figs. 1 and 2a). The relationship between exploratory behavior and calling effort remained significantly correlated when nonexplorers and noncallers were excluded from the analysis (Table 3). Likewise, females that were more exploratory were also

Table 3 Across-context Spearman (r_s) correlations between first principal component scores of all behavioral measures

Sex	Trait 1	Trait 2	All individuals included			Nonperformers excluded		
			r_s	P value	N	r_s	P value	N
Male	Exploration/silent PC1	Mate attraction PC1	<i>-0.3109</i>	<i>0.0066*</i>	71	<i>-0.4243</i>	<i>0.0021*</i>	50
Female	Exploration/silent PC1	Mating/exploration PC1	<i>0.2793</i>	<i>0.0096*</i>	85	0.2311	0.0640	65
Male	Exploration/silent PC1	Activity PC1	-0.1777	0.1444	69			
Female	Exploration/silent PC1	Activity PC1	0.0276	0.8083	80			
Male	Activity PC1	Mate attraction PC1	0.0814	0.5062	69			
Female	Activity PC1	Mating/exploration PC1	-0.0423	0.6083	80			
Male	Antipredatory PC1	Mate attraction PC1	-0.1521	0.2053	71			
Female	Antipredatory PC1	Mating/exploration PC1	0.2123	0.0511	85			
Male	Exploration/silent PC1	Antipredatory PC1	<i>0.3080</i>	<i>0.0090*</i>	71	0.1049	0.5307	38
Female	Exploration/silent PC1	Antipredatory PC1	<i>0.2805</i>	<i>0.0093*</i>	85	<i>0.3448</i>	<i>0.0070*</i>	60
Male	Antipredatory PC1	Activity PC1	-0.0676	0.5809	69			
Female	Antipredatory PC1	Activity PC1	-0.0169	0.8819	80			
Male	Aggression PC1	Mate attraction PC1	0.1559	0.1976	70			
Male	Aggression PC1	Exploration/silent PC1	0.0789	0.5423	70			
Male	Aggression PC1	Activity PC1	-0.0413	0.7538	68			
Male	Aggression PC1	Antipredatory PC1	0.1188	0.3577	70			

Correlations that are significant at a false discovery rate B–Y adjusted $\alpha=0.0141$ ($N=19$ statistical tests) are in italics and marked with an asterisk

more likely to emerge quickly and rapidly touch a speaker playing an acoustic mate attraction call when all individuals were included in the analysis (Table 3; Figs. 1 and 2b). When females who did not emerge from their enclosure in the phonotaxis and/or exploratory treatments were excluded from the analysis, the relationship between exploratory behavior and mating behavior remained, though not significantly (Table 3).

Exploratory behavior was significantly positively correlated with antipredatory behavior in both sexes, provided all nonperforming individuals were included in the analysis (Fig. 2c). More exploratory individuals were less cautious following a predatory event (Table 3; Fig. 1). It is important to note that, when nonperformers were excluded from the analysis, this relationship between exploratory behavior and antipredatory behavior remained consistent for females but not males (Table 3). Exploratory behavior was not correlated with activity in either sex or aggression in males. Likewise, antipredatory behavior was not correlated with any other behavior measured (mate attraction, activity, aggression) in either sex. Activity and aggression were also not correlated with each other or any other behavior measured.

Accounting for age, size, and condition effects

Females were 8% larger and 42% heavier than males. While there was extensive variation among males and females in their body size, weight, and condition, none of

these traits explained any of the behavioral variation observed (all $P>0.05$). There were, however, significant age effects. Older males signaled more often (exhibited higher calling effort) than younger males ($t=6.41$, $df=1.69$; $P<0.0001$); overall, age explained 37% of the variation in male calling effort ($R^2_{\text{adj}} = 0.3702$). Likewise, older females appeared to be more attracted to acoustic mate attraction calls (exhibited shorter emergence times and were quicker to touch the speaker in the exploratory phonotaxis experiments) than younger females ($t=-3.33$, $df=1.83$; $P=0.0012$); overall, age explained 11% of the variation in female phonotaxis exploration ($R^2_{\text{adj}} = 0.1070$). Age did not explain any of the variation in the other behaviors we examined.

Because age significantly influenced our mating behavior measures, we ran a Kendall's nonparametric partial correlations test to ascertain the potential confounding effects of age, size, and condition on the significant behavioral correlations that were shown in Table 3. Male mating and exploratory behaviors remained significantly correlated (Kendall's $T=-0.2205$, $df=1.71$, $P=0.0081$). Furthermore, male exploratory behavior was positively correlated with antipredatory behavior (Kendall's $T=0.1662$, $df=1.71$, $P=0.0452$), though not significantly at the adjusted significance alpha level. Likewise, female mating and exploratory behaviors remained significantly correlated (Kendall's $T=0.1927$, $df=1.85$, $P=0.0100$). Furthermore, female exploratory behavior was positively correlated with antipredatory behavior (Kendall's $T=$

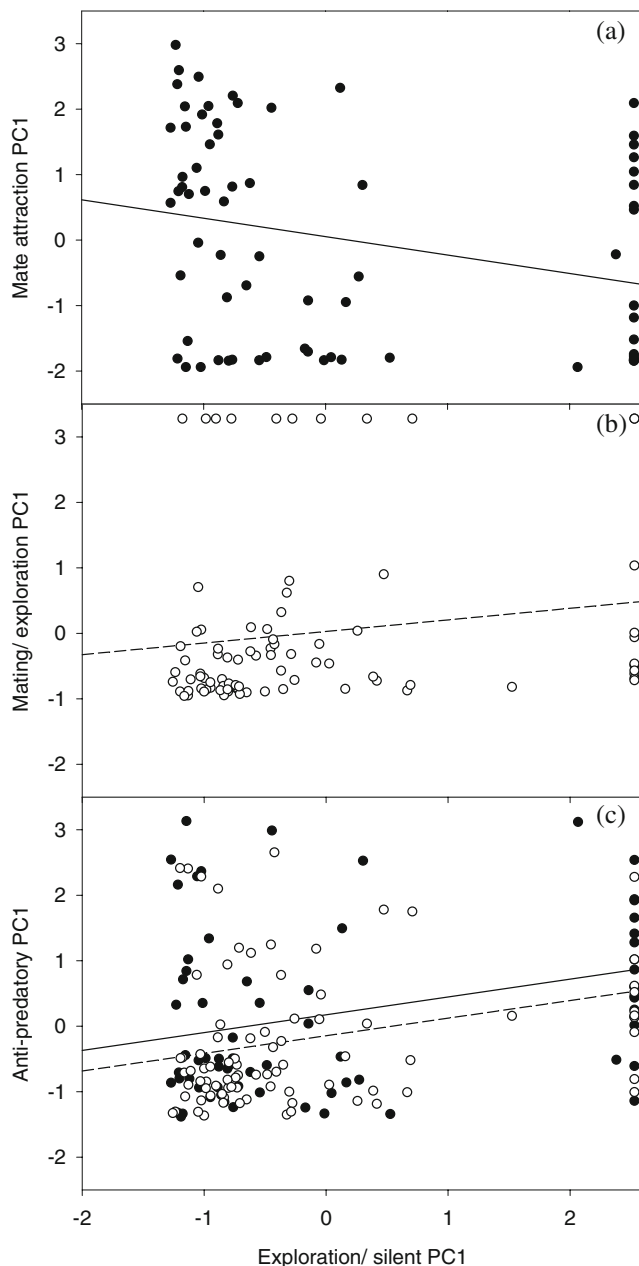


Fig. 2 Observed individual differences in **a** mate attraction (PC1, males only), **b** mating/exploration (PC1; females only), **c** antipredatory behavior (PC1, both sexes) in relation to exploration/silent (PC1) behavior in European house crickets. Each data point represents an individual cricket ($N=71$ or 85 , see Table 3). Open circles and dashed lines represent values for females. Closed circles and solid lines represent values for males. Each line denotes a line-of-best-fit through the relevant data obtained from a least-square regression to illustrate the pattern in the data

0.1824 , $df=1.85$, $P=0.0141$), though not significantly at the adjusted significance alpha level. Overall, these findings support the hypothesis that crickets may exhibit a boldness syndrome because exploratory behavior correlates with mating and antipredatory behavior even when the effects of size, age, and condition are accounted for.

Discussion

Our study investigated behavioral syndromes in both male and female *A. domesticus*. Both sexes appear to exhibit a behavioral syndrome incorporating aspects of exploration and mate attraction. Generally, males that were more exploratory called more than less exploratory males. More exploratory females exhibited stronger phonotactic responses to male mating calls than less exploratory females. Furthermore, both sexes were more willing to emerge quickly following predation events. We characterize this syndrome as a boldness syndrome as individual tendency to take risks and explore a novel environment was central to across-context correlations in behaviors in both males and females.

If behaviors were free to evolve adaptively to independent optima across contexts, then one would expect that bolder individuals would compensate with increased caution when in a predatory situation. Hedrick and Kortet (2006) demonstrated that male *G. integer* calling from a refuge stopped calling and retreated further into the refuge when they sensed the approach of a predator. Similarly, the most conspicuous *G. integer* callers took longer to emerge from a refuge when placed in a novel environment and also stopped calling for longer periods when their calling was interrupted by cues from a potential predator (Hedrick 2000). Indirectly, our results contradict these previous studies as they suggest that males that were bold (in terms of refuge emergence, exploration tendency) were also bold when confronted with a potential predator cue. Furthermore, these bold males also signaled with greater calling effort. What remains unclear, however, is the nature of the relationship between mate attraction and antipredator behavior independent of exploration tendency. The discrepancy between this study and those previous studies may reflect natural interspecific variation arising from genetic constraints or perhaps adaptive responses to local conditions during ontogeny. Alternatively, our findings might be the product of domestication wherein behaviors can be altered by long-term relaxed selection in a captive environment.

Our population of *A. domesticus* has been captive bred for several generations, fed ad libitum, and exposed to a virtually predator-free environment. As such, the *A. domesticus* used in our study have likely experienced very different inbreeding and natural, sexual, and artificial selection pressures from their wild counterparts (Gray 1997, 1999; McDougall et al. 2006). It is, therefore, possible that our findings reflect a domestication syndrome (Moretz et al. 2007). Care must, therefore, be taken when extending our results to wild insect populations. Our findings should, however, be directly comparable to studies of other captive-bred populations and offer useful insights into the nature of possible intertrait correlations

(McDougall et al. 2006). Our study thus provides a useful comparative dataset by which to evaluate the effects of captive breeding on personality traits. Our findings also provide novel insight into the potential mechanistic underpinnings of boldness behavior. Furthermore, our study is the first to consider such a breadth of behaviors in the same individuals of both sexes. Thus, we provide a unique opportunity to view variation across different behavioral contexts and sexes and as such understand the nature of behavioral syndromes in a captive population of crickets.

In addition, our findings with respect to a relationship between age and mating behavior offers further insight into the proximate underpinnings of boldness in male and female crickets. While age differences did not appear to influence most behaviors of interest in our study, they played a prominent role in those trials quantifying mating effort. Older males exhibited a greater calling effort than younger males and older females emerged faster from refuge and explored phonotactic stimulus faster than younger females. Several recent studies have demonstrated that motivational state can greatly influence behavior in crickets, particularly in terms of aggression and mating (Brown et al. 2006, 2007a, b; Killian and Allen 2008). Because males and females were kept individually isolated during trials, it is possible that older individuals exhibited motivational asymmetry from their younger counterparts as a result of this lack of access to potential mates. Reduced access to mates has been shown to increase male–male aggressiveness as well as increase mating frequency relative to males with unfettered access to females (Brown et al. 2007a, b). Similarly, dominance and subordination in males may also be affected by the presence or absence of potential mates. For example, when a previously subordinate male gains mating experience, they may become more dominant over previous winners of aggressive bouts that did not gain copulations prior to later agonistic encounters (Killian and Allen 2008). We did not find any connection between age and aggression nor a relationship between aggression and mating behavior. Nevertheless, the increased tendency of males to take risks by exerting greater calling effort and the increased tendency of females to exit a refuge and touch a speaker broadcasting mate attraction calls suggest that age is an important consideration when studying insect personality.

Our study also investigated differences between the sexes. While females were larger and more active during their activity trials and slightly less cautious following autotomy than males, the two sexes did not differ in their expression of their boldness syndrome. More exploratory males called more than less exploratory males. Likewise, more exploratory females responded quicker to mating calls than less exploratory females. Furthermore, for both males and females, more

exploratory individuals emerged quicker than less exploratory individuals following simulated predation events. These findings suggest that selection may be acting similarly on males and females. For both sexes, the tendency to take risks and explore novel environments remains central to explaining variation in mating and antipredatory behaviors.

While important strides are being made in terms of our understanding of the evolutionary importance of individual-level differences such as those reflected in animal personality traits, significant gaps in our knowledge remain. This is particularly true in terms of the relationship between personality and the effects of captive rearing and domestication in animal populations (Wright et al. 2006; McDougall et al. 2006). This information is particularly relevant as natural, sexual, and artificial selection in captive environments may result in permanent departures in behavioral (and morphological) traits from natural populations (Svartberg and Forkman 2002; Huntingford 2004; McDougall et al. 2006). As such, studies investigating the nature of behavioral correlations across-contexts in captive populations may have important implications for conservation biology as well as captive-breeding programs (McDougall et al. 2006).

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